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Effects of phosphorus availability on later stages of primary succession in Gongga Mountain glacier retreat area

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Head title: Phosphorus affects later stages of primary succession

Highlights

- Intra- and interspecific competition experiments were conducted in *A. fabri* and *P. brachytyla*.
- P fertilization changes the competitive outcomes in these two conifer species.
- P plays an important role in determining asymmetric competition patterns.
- P availability causes a shift in the dominant species during interspecific competition.
- P affects the later stages of primary succession in the Hailuogou glacier retreat area.

Abstract Intra- and interspecific competition and modifications in environmental characteristics are the main drivers of plant community dynamics, but few studies have investigated the combined effects of competition and phosphorus (P) availability on ecological succession. Seedlings of conifers *Abies fabri* and *Picea brachytyla* were collected from the late-stage Hailuogou glacier retreat area and grown under different P regimes (control and P fertilization) to investigate the impact of intra- and interspecific competition on photosynthetic capacity, resource (water, N and P) use efficiency and growth performance in two types of native soil. In the control treatment, there were no differences in the total biomass of *A. fabri* between the two competition patterns under either type of soil, whereas interspecific competition decreased the total biomass of *P. brachytyla* grown in the soil collected from *A. fabri* plots. However, under P fertilization, *A. fabri* individuals exposed to interspecific competition showed a stronger competitive ability, as their total biomass, absolute height growth rate, net photosynthetic rate, water use efficiency ($\delta^{13}C$) and leaf P content were significantly higher under interspecific competition compared to intraspecific competition. No differences in these traits were detected in *P. brachytyla* between the two competition patterns. The results indicated that P plays an important role in determining asymmetric competition patterns among Pinaceae species. The interactive effect of interspecific competition and P availability highlighted here could influence the community composition and dynamics of plants during late-stage primary succession in a glacier retreat area.

Key-words: intra- and interspecific competition; P fertilization; resource use efficiency;

primary succession; Hailuogou glacier retreat area

1. Introduction

Plant soil feedbacks (PSFs) arise from coordinated modifications of biotic and abiotic characteristics of soil by plants. Thus, past changes in soil properties by plants affect subsequent plant growth (Bever, 1994; Bever et al., 1997; Bartelt-Ryser et al., 2005; Ehrenfeld et al., 2005). These feedbacks can have significant impacts on plant performance and abundance, and on the composition of communities as well (Klironomos, 2002; van der Putten et al., 2013; Heinze et al., 2015a). Recent focus on PSFs has highlighted their potential importance in explaining a wide range of ecological phenomena, including exotic invasions (Klironomos, 2002; van Grunsven et al., 2007), coexistence and dominance (Bever et al., 1997; Daufrense and Hedin, 2005), and successional changes (van der Putten et al., 1993; Kardol et al., 2006, 2007). Although the potential importance of PSFs has been widely acknowledged, their environmental interrelationships are poorly understood. A wide range of environmental factors, such as soil structure, water content and initial soil community composition, and especially nutrient availability in soil have the capacity to modify PSFs (Manning et al., 2008).

Competition is considered to be one of the main biotic factors affecting plant growth and physiological processes, thereby modifying the composition of plant communities (Williams and McCarthy, 2001; Nanami et al., 2005; Michalet, 2006; Oksanen et al., 2006; Raynaud et al., 2008). In response to competition, plants display a multitude of

plastic responses to optimize their performance (Pierik et al., 2013). While intraspecific competition occurs at all stages of community development, interspecific competition among species with different physiological and functional responses is prominent and inevitable during the primary succession (Walker and Moral, 2009). Intra- and interspecific competition can affect plants at various organizational levels, consequently resulting in morphological responses and changes in resource allocation (Novoplansky, 2009; Yamawo, 2015). Recent studies have indicated that intra- and interspecific competition may lead to substantial changes in photosynthetic capacity (Poorter et al., 2012), phosphorus (P) absorption (Müller and Bartelheimer, 2013) and water use efficiency ($\delta^{13}C$) (Duan et al., 2014), which in turn facilitate the optimization of plants' performance and affect their competitive status in various environments. Yet, it is still difficult to predict plants' performance during the primary succession in glacier retreat areas, where multiple environmental factors, including various soil properties and aboveground environmental characteristics, change simultaneously to create complex interactions.

Abiotic factors can substantially alter competitive interactions (Maestre et al., 2009; Hart and Marshall, 2013), e.g. competition outcomes can change along with nutrient availability in soil (Gerdol et al., 2000; Sans et al., 2002). Competition for soil nutrients has been considered as a major factor that determines the distribution of plant species (Silvertown, 2004; Thuiller et al., 2008). Among soil mineral nutrients, phosphorus often limits reproductive and vegetative growth of plants in terrestrial ecosystems (Elser

et al., 2007; Vitousek et al., 2010). Phosphorus is a key mineral nutrient involved in plant metabolism, such as photosynthetic carbon assimilation and protein synthesis (Sterner and Elser, 2002), and its availability affects species diversity, plant competitiveness, growth and physiological activities (Williamson et al., 2001; Turnbull et al., 2007; Lambers et al., 2011). However, studies on how P absorption is influenced by interactions with neighbors and how intra- and interspecific competition are altered by changes in P availability during primary succession are still limited (but see Tilman, 1993; Brais et al., 1995), especially concerning glacier retreat areas.

The Hailuogou glacier retreat area, located on the south-eastern fringe of the Tibetan Plateau, has developed a complete primary succession series from bare land to climax vegetation communities, thus providing an excellent place to study the relationships between vegetation succession and soil development (Luo et al., 2012; Prietzel et al., 2013a, 2013b; Zhou et al., 2013; Lei et al., 2015). Researchers have divided the primary succession series into 7 long-term primary succession stages, in which the community of stage 6 (soil age spanning between 50–80 years) is dominated by *Abies fabri*, and the climax community of stage 7 (from 80 to 120 years) is dominated by *Picea brachytyla*. During succession in a glacier retreat area, soil water availability gradually reduces, as the distance from the glacier increases and water consumption by vegetation increases, while P availability decreases significantly from stage 6 to stage 7 (Zhou et al., 2013; Lei et al., 2015). Thus, there may be a trade-off between water and phosphorus use efficiencies (Jones et al., 2005; Liu et al., 2015). Therefore, species-specific resource

absorption strategies could ultimately determine the competition outcomes of *A. fabri* and *P. brachytyla*, possibly being responsible for the successional replacement of *A. fabri* by *P. brachytyla* in the Hailuogou glacier retreat area.

Here, we investigated the performance of two evergreen conifer species, *A. fabri* and *P. brachytyla* (Pinaceae), in the Hailuogou glacier retreat area to examine the effect of P fertilization on plant soil feedbacks (PSFs), and on intra- and interspecific competition during primary succession. To gain an insight into physiological and functional traits that affect the competitive capacity of *A. fabri* and *P. brachytyla*, responses of growth characteristics, net photosynthetic rate (P_n), photosynthetic N and P use efficiencies (PNUE, PPUE), foliage carbon isotope composition ($\delta^{13}C$) and non-structural carbohydrate contents to intra- and interspecific competition and P fertilization were analyzed in two types of native soils. The following hypotheses were tested: (i) P fertilization modifies plant soil feedbacks (PSFs); (ii) *A. fabri* and *P. brachytyla* utilize different competitive strategies under interspecific competition and P fertilization; (iii) due to different physiological and functional traits of these two conifers, changes in soil P availability result in asymmetric competition outcomes among competing *A. fabri* and *P. brachytyla* individuals. Thus, P could play a pivotal role in determining the plant community composition and dynamics during the late-stage primary succession in the Hailuogou glacier retreat area.

2. Materials and methods

2.1. Study site and plant material

The study was conducted at the Gongga Mountain Alpine Ecosystem Observation and Experiment Station of the Chinese Academy of Sciences, located on the south-eastern fringe of the Tibetan Plateau (elevation: 3000 m a.s.l; 29°34' N, 101°59' E). The mean annual temperature is 4.2 °C and mean annual precipitation 1947 mm (averages for 22 years). The Hailuogou glacier retreat area is 2 km away from the station and the climatic conditions are similar. Two types of native soil were used and obtained from the natural habitats of the two species: one collected from plots dominated by *A. fabri* (successional stage 6) and the other type from the plots dominated by *P. brachytyla* (successional stage 7). The total P content of the soil collected from the plots dominated by *A. fabri* (average ± SE = 0.90 ± 0.02 g kg^{-1}) was significantly higher ($P < 0.001$) than that from *P. brachytyla* plots (0.57 ± 0.03 g kg^{-1}).

2.2. Experimental design

The study was divided into two parts. The aim of the first part was to investigate plant soil feedbacks (PSFs). During mid-September of 2014 (to allow adaptation to the environment, seedlings were planted seven months before P fertilization treatments

were carried out), healthy *A. fabri* and *P. brachytyla* seedlings with a height of about 25 cm were selected from a nursery near the station and planted in plastic pots (plants grown alone; one seedling per pot). Each pot had an external diameter of 32 cm and a height of 25 cm. *A. fabri* and *P. brachytyla* grown alone in two different soils were subjected to two P fertilization supply levels (control, 0 g P; P fertilization, 0.4 g P per pot; altogether 4 soil × P fertilization treatment combinations). Twenty replicates per treatment were included in the experiment. The experiment was performed outside in the field in natural rain conditions. P fertilization was provided as NaH_2PO_4 at 0.4 g P per pot, i.e. 50 kg P ha^{-1} $year^{-1}$ in every P-fertilized treatment (Siddique et al., 2010; Chen et al., 2015). Plants were watered every other day. The seedlings were fertilized on 6 May 2015 and harvested on 28 August 2015. The fluctuating conditions over the experimental period (from 6 May to 28 August 2015) were as follows: light net radiation range of 20.4 – 1534.2 W/m^2, the temperature range of -0.36 – 21.88 °C and the relative humidity range of 36 – 100%.

In the second part of the study, the experimental layout was completely randomized with four factors (species, competition, soil type and P fertilization). Two P fertilization supply levels (control, 0 g P; P fertilization, 0.4 g P per pot), two species (*A. fabri* and *P. brachytyla*), two competition patterns (intraspecific competition: *A. fabri* × *A. fabri*, or *P. brachytyla* × *P. brachytyla*; interspecific competition: *A. fabri* × *P. brachytyla*) and two types of native soil were established (altogether 16 treatment combinations). During mid-September of 2014, healthy *A. fabri* and *P. brachytyla* seedlings with a height of

about 25 cm were selected and planted in plastic pots (two seedlings per pot: two *A. fabri*, two *P. brachytyla* or one *A. fabri* and one *P. brachytyla*). The second part of the experiment was conducted similarly as the first part, except for the competition treatment.

2.3. Determination of growth characteristics

Plant height was monitored weekly during the experiment. Height was measured from the stem base to the top of the plant. The absolute height growth rate (AGR, cm d^{-1}) was calculated as AGR = ($height_2$ – $height_1$) / (t_2 – t_1), where the denominator is the time elapsed between the initial and final measurements. At the end of the experiment, five plants from each treatment were selected randomly for biomass measurements. The selected plants were harvested and divided into leaves, stems and roots. Biomass samples were dried at 70 °C for 72 h and their dry mass was determined.

2.4. Determination of plant soil feedback responses

The biomass of plants grown alone (Fig. S1) was used to determine PSFs. A relative interaction index (Armas et al., 2004; Perkins and Nowak, 2012) was adapted to calculate the net effect of soil conditions (PSFs response, R_{PSFs}). The formula for PSFs response is $R_{PSFs} = (B_c - B_a) / (B_c + B_a)$, where B_c is the biomass of each species growing alone under the "self" soil condition type, and B_a is the mean biomass of that species

under all “other” soil condition types. For example, if species A grew to 10 g in “self” soil and to 15 g in “other” soil, then species A would have a R_{PSFs} of –0.20 [i.e., (10–15)/(10+15) = –0.20]. A positive value indicates that a plant produced more biomass due to the soil condition, and a negative value indicates that a plant produced less biomass.

2.5. Determination of N and P contents for leaf and root samples

At the end of the experiment, leaf and root samples for N and P analyses were sampled from five randomly chosen individuals in each treatment. Dried samples were ground into fine powder and passed through a mesh (pore diameter ca. 275 μm). N contents were determined by a semi-micro Kjeldahl method (Mitchell, 1998), and P contents by induced plasma emission spectroscopy (Hötscher and Hay, 1997).

2.6. Determination of net photosynthetic rates

The light-saturated net photosynthetic rate (P_n) of current-year intact leaves was measured with the LI-COR 6400 portable photosynthesis measuring system (LI-COR, Lincoln, NE, USA) at the end of July 2015. Five randomly chosen individuals in each treatment were selected for P_n measurements, and the measurements were taken between 08:00 and 11:30. A conifer type chamber (PLC-broad, PP Systems) was used, and the standard measurement conditions were as follows: leaf temperature, 25 °C; air

vapor pressure deficit, 1.5 ± 0.5 kPa; relative humidity, 50%; light intensity (PPFD), 1500 μmol m^{-2} s^{-1}; and CO_2 concentration, 400 ± 5 μmol mol^{-1}. Once the gas exchange rates stabilized, the steady-state data were recorded. P_n was calculated on a leaf dry mass basis, and the mass-based photosynthetic N and P use efficiencies (PNUE, PPUE) were calculated as ratios between the mass-based photosynthetic rate and leaf nitrogen and phosphorus contents.

2.7. Determination of non-structural carbohydrates

At the end of the experiment, the leaf and root samples for non-structural carbohydrate analyses were sampled from five randomly chosen individuals in each treatment. Total soluble sugar and starch contents in glucose equivalents were determined by the anthrone method according to Yemm and Willis (1954). The dry leaf and root samples were incubated in 80% (v/v) ethanol at 80 °C for 30 min, and centrifuged at 5000 g for 10 min. The ethanol extract was used for the determination of total soluble sugar contents. The residue was further hydrolysed with 9.2 mol L^{-1} $HClO_4$ for 30 min, and centrifuged at 5000 g for 15 min. The extract solution was used for the starch content analysis. Additional details concerning the extraction assay are given in Guo et al., (2016).

2.8. Determination of carbon isotope composition

The carbon isotope composition ($\delta^{13}C$) was determined for the same leaves, which had been used for the P_n estimation. Leaf samples were oven-dried at 70 °C for 72 h. Dried leaves were ground, and $^{13}C/^{12}C$ ratios were determined with an isotope ratio mass spectrometer (Thermo Fisher Scientific, Inc., USA). The carbon isotope composition was expressed as $\delta^{13}C$ values. The overall precision of the $\delta^{13}C$ values was better than 0.1‰, as determined by repetitive samples. The $\delta^{13}C$ values were reported relative to the international standard, Pee Dee Belemnite (PDB). The entire analysis was performed in the Stable Isotope Laboratory for Ecological and Environmental Research, Chinese Academy of Forestry.

2.9. Statistical analyses

The statistical analyses were carried out with the Statistical Package for the Social Sciences (SPSS, Chicago, IL, USA) version 18.0. Before statistical analyses, data were checked for normality and the homogeneity of variances and log-transformed to correct for deviations from these assumptions when needed. Individual differences among means were determined by Tukey's HSD tests of one-way ANOVAs. Three-way ANOVAs were used to test for the effects of soil, competition, phosphorus and their interactions. All statistical effects were considered significant at $P < 0.05$. A principal component analysis (PCA) with all variables was further undertaken to gain insight into the variable loadings as dependent on competition, P fertilization and soil types, and differences in eco-physiological traits. PCA analyses were performed using Canoco 5.0

(Microcomputer Power, USA).

3. Results

3.1. Effects of P fertilization on plant soil feedback responses

In the control treatment, both *A. fabri* and *P. brachytyla* experienced negative PSF responses in both types of native soil. However, when exposed to P fertilization, the two conifer species (especially *A. fabri*) experienced positive PSF responses in both types of native soil (Fig. 1).

3.2. Effects of competition patterns and P fertilization on growth characteristics

In the control treatment, there were no differences in the total biomass of *A. fabri* between the two competition patterns under either type of soil, whereas interspecific competition decreased the total biomass of *P. brachytyla* grown in the soil collected from *A. fabri* plots (Fig. 2a). Upon P fertilization, *A. fabri* had a higher total biomass under interspecific competition than under intraspecific competition, but the total biomass of *P. brachytyla* showed no difference between intra- and interspecific competition in either type of soil (Fig. 2a). Under P fertilization, both species possessed higher absolute height growth rates (AGR) but lower root/shoot ratios than when grown without P fertilization, and *A. fabri* had the highest AGR under interspecific competition

in both types of soil (Fig. 2b, c). The competition × phosphorus interaction significantly affected the total biomass, AGR and root/shoot ratio of *A. fabri*, while the soil × competition interaction significantly affected the total biomass of both species.

3.3. Effects of competition patterns and P fertilization on photosynthetic capacity and resource use efficiency

In the P fertilization treatment, *A. fabri* had higher P_n and $\delta^{13}C$ under interspecific competition than under intraspecific competition, but in *P. brachytyla*, these traits did not differ between intra- and interspecific competition when grown in either type of soil (Fig. 3a, d). P fertilization increased PNUE of *A. fabri* but it had no effect on *P. brachytyla* in any treatments (Fig. 3b). Under P fertilization, PPUE of *A. fabri* was unchanged, but PPUE of *P. brachytyla* declined in both soil conditions (Fig. 3c). The soil × competition and competition × phosphorus interactions significantly affected P_n of *A. fabri*, and the competition × phosphorus interaction significantly affected $\delta^{13}C$ of both species.

3.4. Effects of competition patterns and P fertilization on non-structural carbohydrates

Under P fertilization, *A. fabri* subjected to interspecific competition possessed higher soluble sugar and starch contents in roots compared to intraspecific competition. However, *P. brachytyla* subjected to interspecific competition showed a significant

decline in soluble sugar and starch contents of roots when compared to intraspecific competition when using the soil collected from *P. brachytyla* plots (Fig. 4a, b). P fertilization decreased soluble sugar and starch contents in leaves and roots of both species when soil collected from *A. fabri* plots was used (Fig. 4a, b). The soil × competition × phosphorus interaction significantly affected soluble sugar and starch contents in leaves and roots of *P. brachytyla*, and the soil × phosphorus and competition × phosphorus interactions significantly affected soluble sugar and starch contents in the leaves and roots of both species.

3.5. Effects of competition patterns and P fertilization on N and P contents

A. fabri subjected to interspecific competition without P fertilization had higher leaf nitrogen and phosphorus contents when compared to intraspecific competition in the soil collected from *A. fabri* plots, while the opposite result was found in *A. fabri* grown in the soil collected from *P. brachytyla* plots. However, these traits showed no differences in *P. brachytyla* between the two competition patterns and two types of soil (Fig. 5a, b). Upon P fertilization, *A. fabri* had a higher leaf phosphorus content under interspecific competition than under intraspecific competition, but *P. brachytyla* showed no differences between intra- and interspecific competition under any type of soil (Fig. 5a, b). The soil × competition, competition × phosphorus and soil × competition × phosphorus interactions significantly affected nitrogen and phosphorus contents in the leaves of *A. fabri*.

3.6. Relationships among studied traits under different competition treatments and P fertilization

The principal component analysis (PCA) showed a clear delineation according to trait combinations in intra- and interspecific competition treatments in *A. fabri* and *P. brachytyla* under different P regimes and soil types (Fig. 6). The PCA model with two components explained 78.34% of the total variance of *A. fabri* (Fig. 6a) and 79.19% of the total variance of *P. brachytyla* (Fig. 6b). In *A. fabri*, the first component (51.20%) was strongly influenced by PNUE, P_n, total biomass, root and leaf N, root and leaf P, root and leaf starch, and root and leaf soluble sugars, while the second component (27.14%) was strongly influenced by R/S ratio, PPUE and AGR. In *P. brachytyla*, the first component (55.67%) was strongly influenced by PNUE, R/S ratio, PPUE, root and leaf N, root and leaf P, AGR, P_n, total biomass, root and leaf soluble sugars, and leaf starch, while the second component (23.52%) was strongly influenced by root starch. In addition, leaf N, leaf P, root N, root P and PNUE showed positive correlations with the total biomass and P_n of both species.

4. Discussion

4.1. P fertilization affects plant soil feedbacks

In our experiment, seedlings of *A. fabri* and *P. brachytyla* from the later stages of primary succession varied in their PSFs responses to P fertilization. In the control treatment, both *A. fabri* and *P. brachytyla* experienced negative PSFs, but when exposed to P fertilization, the two conifer species experienced positive PSFs in both types of native soil (Fig. 1). The reason for the species experiencing negative PSFs may be that the P content of soil cannot meet the demands for growth. Previous studies have found that positive PSFs are expected to increase species abundance, persistence and invasiveness (Callaway and Aschehoug, 2000; Eppstein et al., 2006; Inderjit and van der Putten, 2010), while negative PSFs are expected to decrease species abundance and persistence, increase successional replacements and maintain species diversity (van der Putten et al., 1993; Klironomos, 2002; Kardol et al., 2006; Petermann et al., 2008). For example, negative PSFs have been found to drive plant community dynamics within sand dune communities, where negative PSFs appear to contribute to species replacement during succession rather than to long-term coexistence (van der Putten et al., 1993). In line with these observations, Kardol et al., (2006) found that temporal variation in plant-soil feedback controls succession. Thus, our finding of negative PSFs

under the control treatment suggests that modifications in soil characteristics could decrease species abundance and maintain species diversity. However, P fertilization altered PSFs from negative to positive, which could increase plant biomass and persistence, and influence plant community composition and dynamics during the late-stage primary succession in the Hailuogou glacier retreat area.

4.2. Competition pattern and P fertilization affect growth

In this study, significant species-specific responses in growth and biomass accumulation were detected in plants under intra- and interspecific competition and P fertilization when grown in two types of soil. Furthermore, multiple significant interactive effects of treatment factors on growth traits were discovered (Fig. 2). The present study revealed that P fertilization alters growth traits differently in *A. fabri* and *P. brachytyla* in the presence of intra- and interspecific competition. When grown without P fertilization, there were no differences in the total biomass of *A. fabri* between the two competition patterns under either type of soil, whereas interspecific competition decreased the total biomass of *P. brachytyla* in the soil collected from *A. fabri* plots (Fig. 2a). These findings indicated that when grown in the soil collected from *A. fabri* plots, *A. fabri* is a better competitor than *P. brachytyla*. When P-fertilized, *A. fabri* had a higher total biomass under interspecific competition than under intraspecific competition, while in *P. brachytyla* no difference was found between intra- and interspecific competition under either type of soil (Fig. 2a). These findings indicated that under P fertilization, *A. fabri*

is a better competitor and benefits from the presence of *P. brachytyla* in both types of soil, overall suggesting that *A. fabri* and *P. brachytyla* utilize different growth strategies under different P regimes.

Many studies have shown that plants can alter their root-shoot allocation in response to environmental conditions (Gedroc et al., 1996; Zhao et al., 2012; Chen et al., 2014; Guo et al., 2016). The present study showed that both studied species had higher root/shoot ratios under the control treatment (Fig. 2c). This result is consistent with previous studies suggesting that plants invest relatively more in roots in low-nutrient soils. Such a plastic response allows for more efficient capture of limited soil resources, thereby enhancing plants' competitive capacity (Fichtner and Schultze, 1992; Walters and Reich, 2000; Shipley and Meziane, 2002; Portsmuth and Niinemets, 2007). In addition, previous studies have indicated that in P-limited conditions, relative growth rates can increase sharply with increasing leaf P contents (Burns et al., 1997; De Groot et al., 2001a), and that P addition can significantly alter competitive interactions (Michelle and Janos, 2004; Sardans et al., 2004; Forrester et al., 2006; Ahmad-Ramli et al., 2013). Our results showed that under P fertilization, *A. fabri* subjected to interspecific competition had higher AGR and leaf P contents than when subjected to intraspecific competition in either type of soil (Fig. 2b, 5b).

4.3. Competition pattern and P fertilization affect photosynthetic capacity and resource use efficiencies

The present study indicated that under P fertilization *A. fabri* subjected to interspecific competition had a higher mass-based light-saturated net photosynthetic rate (P_n) and leaf P content than under intraspecific competition, while in *P. brachytyla* there were no differences between intra- and interspecific competition (Fig. 3a, 5b). In line with our observations, P_n has been found to be positively correlated with leaf P contents in various plant species (Wright et al., 2004; Hidaka and Kitayama, 2009). Furthermore, PNUE and PPUE have been considered to be important functional traits that characterize species in relation to their leaf economics strategy (Hikosaka, 2004; Hidaka and Kitayama, 2009). In our study, P fertilization significantly increased PNUE of *A. fabri* but it had no effect on PNUE of *P. brachytyla* in any competition or soil conditions (Fig. 3b). Reich et al. (1994) have studied photosynthesis-nitrogen relations in Amazonian tree species and found that climax species tend to have low PNUE, which corresponds to our results showing that AGR of *A. fabri* was higher than that of *P. brachytyla* under P fertilization (Fig. 2b). Given that high PNUE is associated with a high relative growth rate (Poorter et al., 1990; Garnier et al., 1995), we may expect that species with high PNUE would outcompete those with low PNUE. However, succession can alter the whole environmental complex, and as our results demonstrate, changes in soil characteristics are a key factor that reduces the superior competitive capacity of the higher PNUE species *A. fabri* at later stages of succession.

Increased PPUE is an important functional trait in trees growing in P-poor soils (Denton

et al., 2007), but enhanced PPUE is not always observed in low P soils. Cordell et al. (2001a, b) found that there were no differences in PPUE of *Metrosideros polymorpha* (Myrtaceae) between N-limited and P-limited Hawaiian forests. The present study showed that under P fertilization, *A. fabri*, unlike *P. brachytyla*, was able to maintain a relatively high PPUE when compared to unfertilized individuals (Fig. 3c). In addition, under P fertilization, $\delta^{13}C$ of *A. fabri* was significantly higher in interspecific competition compared to intraspecific competition, while $\delta^{13}C$ of *P. brachytyla* showed no difference between the two competition patterns (Fig. 3d). Thus, *A. fabri* growing under interspecific competition and with P fertilization had a higher water use efficiency, similarly to observations in other species (Farquhar et al., 1982; Duan et al., 2014; Dong et al., 2015; Guo et al., 2016). Furthermore, the PCA analysis indicated positive correlations among total biomass, P_n and PNUE (Fig. 6). The capacity to use P is advantageous when P is available, but when P becomes increasingly limited through succession, the competitive advantage is lost.

4.4. Competition pattern and P fertilization affect non-structural carbohydrates

Storage of non-structural carbohydrates, such as starch and sugars that can be mobilized, is thought to be critical for survival under stress and disturbance, particularly in long-lived trees (Palacio et al., 2014). Such storage provides a carbon buffer when respiratory growth or other physiological demands are not synchronized with photosynthesis. For instance, high non-structural carbohydrate contents of roots could

provide assimilation energy for nutrient uptake (Kobe et al., 2010; Pokhilko et al., 2014). However, carbohydrate contents can also increase when environmental stress inhibits growth (sink) more than photosynthesis (source) (Paul and Stitt, 1993; Wang and Tillberg, 1997). A lower investment of photosynthetic carbon in growth and a greater investment in carbon storage may be an adaptation mechanism that adjusts acquisition and recycling of P resources to seasonal growth demands. Non-structural carbohydrate reserves built up during past growing seasons are a carbon source for respiration during dormancy, endow frost tolerance (Kozlowski, 1992), and are used for the construction of leaves and fine roots at the beginning of a new growing season (Chapin et al., 1990; Loescher et al., 1990; Kozlowski, 1992; Gaucher et al., 2005). We observed that soluble sugar and starch contents of both studied species tended to decrease under P fertilization in the soil collected from *A. fabri* plots (Fig. 4a, b), thus indicating less limited sink activities. On the other hand, increased root soluble sugar and starch contents, and possibly a greater capacity for nutrient uptake were possible causes for the better competitiveness of *A. fabri* under interspecific competition and P fertilization. Under P fertilization, *A. fabri* subjected to interspecific competition had higher soluble sugar and starch contents in roots compared to intraspecific competition. However, *P. brachytyla* subjected to interspecific competition showed a significant decline in soluble sugar and starch contents of roots when compared to intraspecific competition in the soil collected from *P. brachytyla* plots (Fig. 4a, b).

Our research suggests that the competitive strength of *A. fabri* exposed to P fertilization

could be attributed to a suite of intrinsic physiological traits. Based on PCA, we found that leaf P and PNUE have positive correlations with the total biomass and P_n of both species. These two parameters may cause the superior competitiveness of *A. fabri* compared to *P. brachytyla* under P fertilization. In general, *A. fabri* displayed a competitive advantage when growing with *P. brachytyla* in both types of soil under P fertilization. High ability to keep carbon balance (e.g., higher water use efficiency ($\delta^{13}C$) and P_n), higher PNUE, as well as the better N acquisition ability make *A. fabri* trees better competitors when compared to *P. brachytyla* under P fertilization. Although the soils used in the study were native soils and obtained from the natural habitats of the two species, they were different from the natural conditions (e.g. physical structure). However, caution is necessary when extrapolating our findings to very complex field situations. Yet, the present new information is helpful when aiming to accurately predict the responses of terrestrial ecosystems to nutrient addition.

5. Conclusions

This study demonstrated that intra- and interspecific competition and P fertilization differently affect the physiological and functional traits of *A. fabri* and *P. brachytyla*, and P fertilization changes the competitive outcomes between these two conifer species. When grown without P fertilization, there were no differences in the total biomass of *A. fabri* between the two competition patterns under either type of soil, whereas interspecific competition decreased the total biomass of *P. brachytyla* in the soil collected from *A. fabri* plots. However, under P fertilization, *A. fabri* displayed a competitive advantage when growing with *P. brachytyla* under either type of soil. These results indicated that P could play an important role in determining asymmetric competition patterns among Pinaceae species. Our results showed that changes in soil P availability and soil feedback coupled with shifts in interspecific competition relationships could influence plant community composition and dynamics in glacier retreat areas.

Author Contribution Statement Lei Yu, the first author of the paper, the main responsibility for data collection, analysis and writing; Mengya Song and Yanbao Lei, significant contributions to data collection and analysis; Baoli Duan and Frank Berninger, significant contributions to data collection and experimental arrangements; Helena Korpelainen and Ülo Niinemets, significant contributions to the interpretation of data and manuscript preparation; Chunyang Li, the corresponding author, the overall responsibility for experimental design and project management.

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Figure legends

Figure 1 Plant soil feedbacks (PSFs) of *A. fabri* and *P. brachytyla* grown alone under different P regimes and soil conditions. A positive value indicates that a plant produced more biomass under a given soil treatment than its mean biomass in all "other" soil treatments. Each value is the mean ± SE (n=5). Different lowercase and uppercase letters indicate significant treatment effects on *A. fabri* and *P. brachytyla*, respectively, according to Tukey's HSD test at a significance level of $P< 0.05$.

Figure 2 Growth characteristics of *A. fabri* and *P. brachytyla* under different competition patterns, P regimes and soil conditions. (a) Total biomass, (b) absolute height growth rate, and (c) root/shoot ratio. Each value is the mean ± SE (n=5). Different lowercase and uppercase letters indicate significant treatment effects on *A. fabri* and *P. brachytyla*, respectively, according to Tukey's HSD test at a significance level of $P< 0.05$. Three-way analyses of variance (ANOVA) were applied to evaluate the effects of different factors and their interactions. S, soil effect; C, competition effect; P, P fertilization effect; S × C, soil × competition effect; S × P, soil × P fertilization effect; C × P, competition × P fertilization effect; S × C × P, soil × competition × P fertilization effect.

Figure 3 Photosynthetic characteristics of *A. fabri* and *P. brachytyla* leaves under

different competition patterns, P regimes and soil conditions. (a) Net photosynthetic rate per dry mass (P_n), (b) photosynthetic nitrogen use efficiency (PNUE), (c) photosynthetic phosphorus use efficiency (PPUE), and (d) $\delta^{13}C$. Each value is the mean ± SE (n=5). Treatment codes and statistical analyses as in Fig. 2.

Figure 4 Non-structural carbohydrate contents in different organs of *A. fabri* and *P. brachytyla* under different competition patterns, P regimes and soil conditions. (a) Soluble sugar content, and (b) starch content. Each value is the mean ± SE (n=5). CK, control treatment; P, P fertilization treatment. The bars without and with oblique lines denote intraspecific and interspecific competition, respectively. Treatment codes and statistical analyses as in Fig. 2.

Figure 5 Nitrogen (N) (a) and phosphorus (P) (b) contents per dry mass in different organs of *A. fabri* and *P. brachytyla* under different competition patterns, P regimes and soil conditions. Each value is the mean ± SE (n=5). CK, control treatment; P, P fertilization treatment. The bars without and with oblique lines denote intraspecific and interspecific competition, respectively. Treatment codes and statistical analyses as in Fig. 2.

Figure 6 Principal component analysis (PCA) based on eco-physiological traits of *A. fabri* and *P. brachytyla* under different competition patterns, P regimes and soil types. P_n, net photosynthesis rate; leaf P, leaf P content; leaf N, leaf N content; root N, root

N content; root P, root P content; leaf starch, leaf starch content; root starch, root starch content; leaf soluble sugar, leaf soluble sugar content; root soluble sugar, root soluble sugar content (all traits expressed on dry mass basis); AGR, absolute height growth rate; R/S ratio, root/shoot ratio.

Figure 1

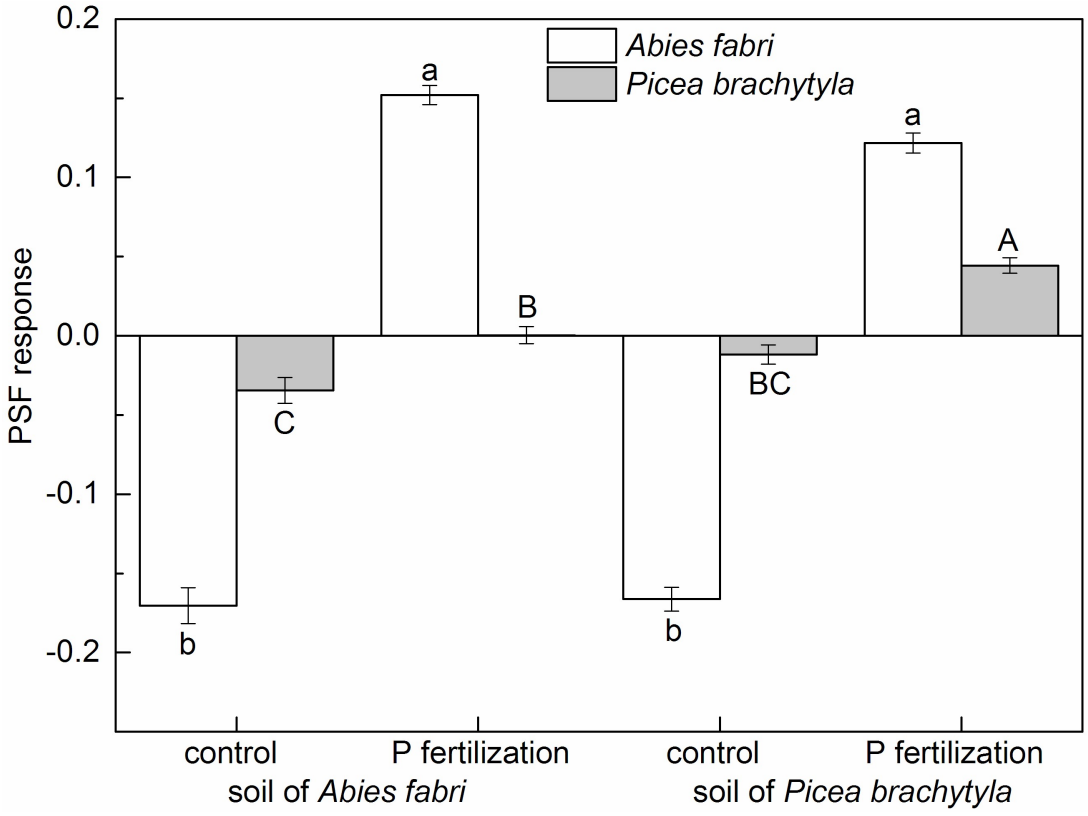

0.2
0.1
0.0
-0.1
-0.2
PSF response
Abies fabri
Picea brachytyla
a
B
C
b
BC
b
a
A
control
P fertilization
control
P fertilization
soil of Abies fabri
soil of Picea brachytyla

Figure 2

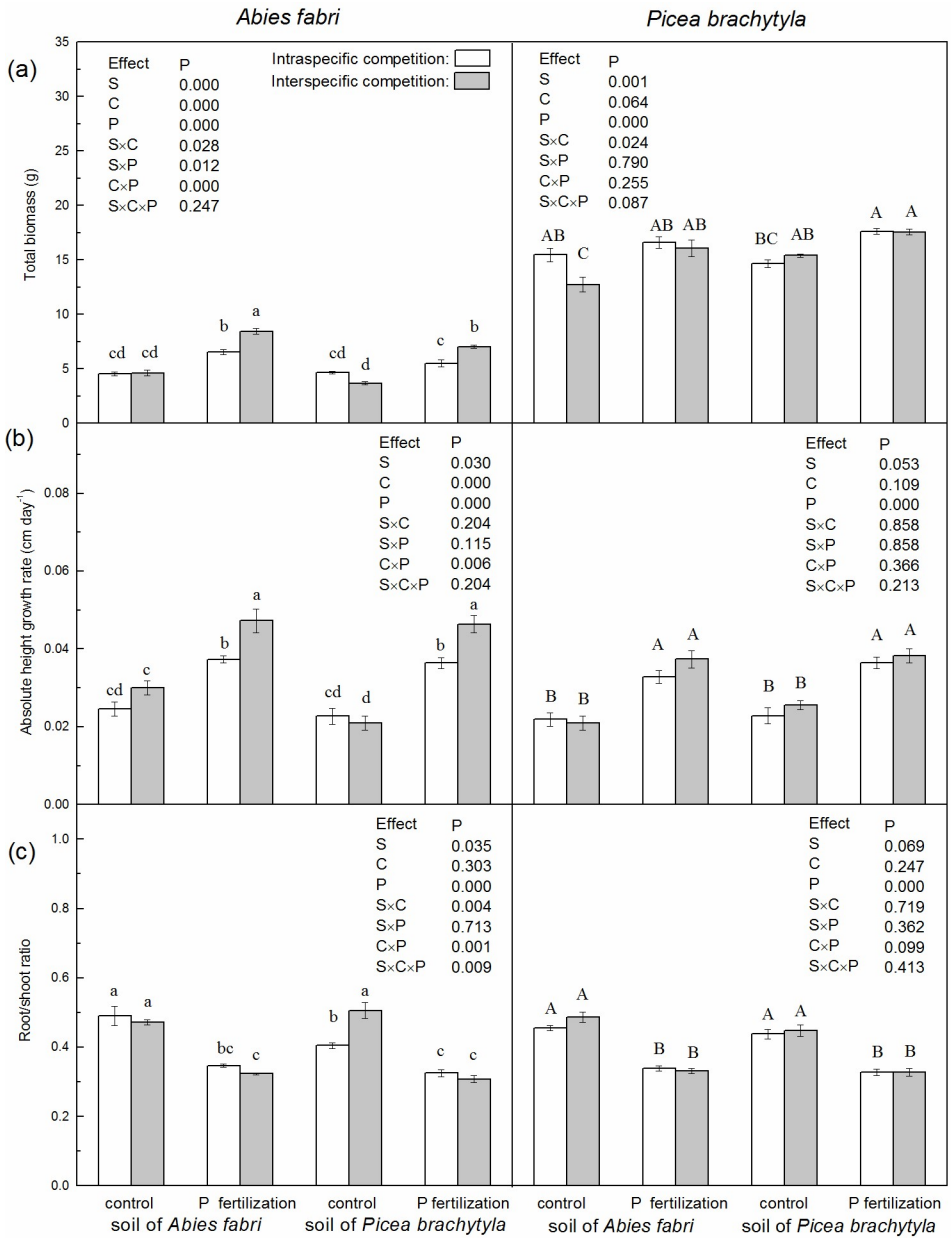

Abies fabri
Picea brachytyla
(a)
(b)
(c)
Intraspecific competition:
Interspecific competition:
Effect P
S 0.000
C 0.000
P 0.000
S×C 0.028
S×P 0.012
C×P 0.000
S×C×P 0.247
Effect P
S 0.001
C 0.064
P 0.000
S×C 0.024
S×P 0.790
C×P 0.255
S×C×P 0.087
Total biomass (g)
Effect P
S 0.030
C 0.000
P 0.000
S×C 0.204
S×P 0.115
C×P 0.006
S×C×P 0.204
Effect P
S 0.053
C 0.109
P 0.000
S×C 0.858
S×P 0.858
C×P 0.366
S×C×P 0.213
Absolute height growth rate (cm day-1)
Effect P
S 0.035
C 0.303
P 0.000
S×C 0.004
S×P 0.713
C×P 0.001
S×C×P 0.009
Effect P
S 0.069
C 0.247
P 0.000
S×C 0.719
S×P 0.362
C×P 0.099
S×C×P 0.413
Root/shoot ratio
control
P fertilization
control
P fertilization
soil of Abies fabri
soil of Picea brachytyla
control
P fertilization
control
P fertilization
soil of Abies fabri
soil of Picea brachytyla

Figure 3

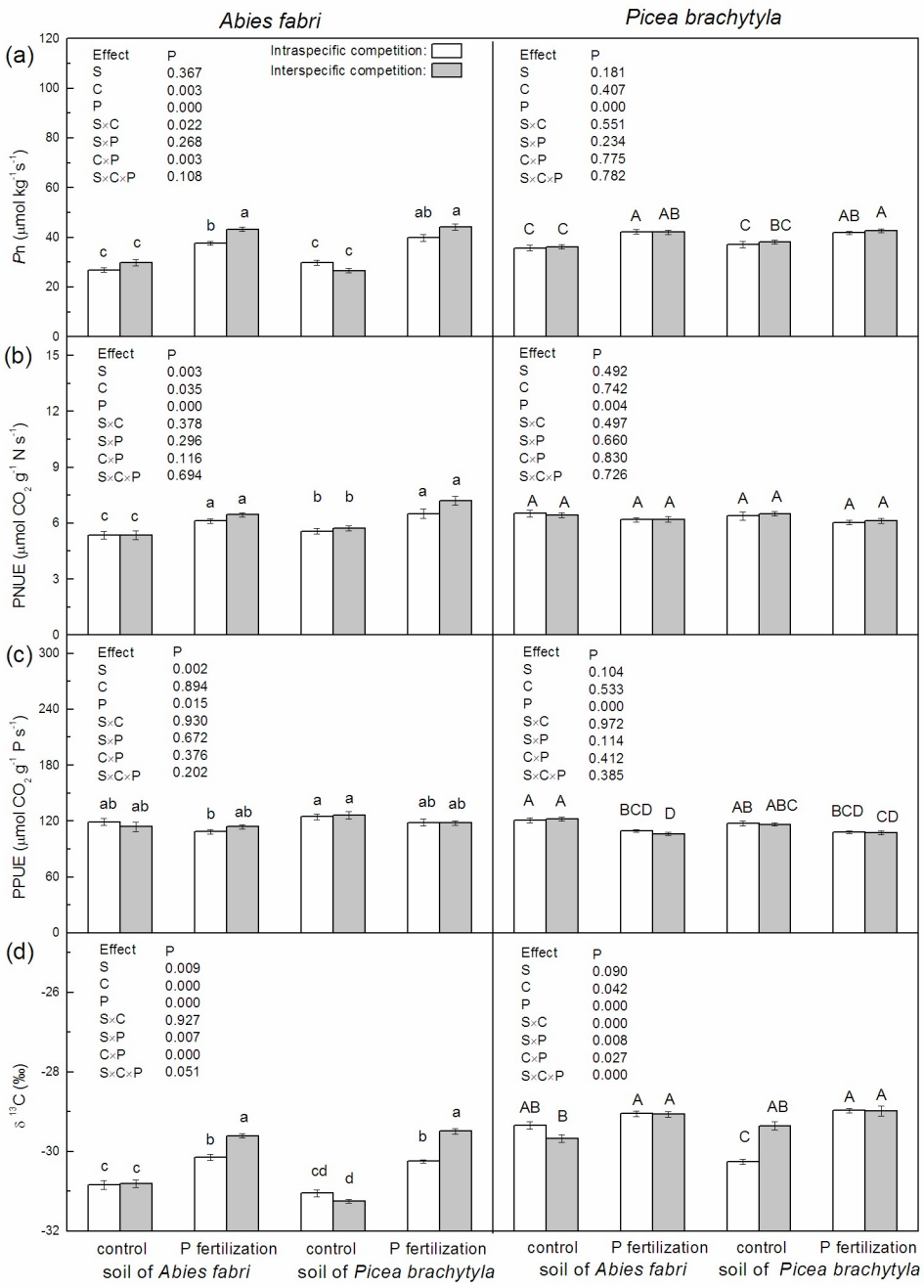

Abies fabri
Picea brachytyla
(a)
(b)
(c)
(d)
Intraspecific competition:
Interspecific competition:
Pn (μmol kg-1 s-1)
PNUE (μmol CO2 g-1 N s-1)
PPUE (μmol CO2 g-1 P s-1)
δ 13C (‰)
Effect P
S 0.367
C 0.003
P 0.000
S×C 0.022
S×P 0.268
C×P 0.003
S×C×P 0.108
Effect P
S 0.181
C 0.407
P 0.000
S×C 0.551
S×P 0.234
C×P 0.775
S×C×P 0.782
Effect P
S 0.003
C 0.035
P 0.000
S×C 0.378
S×P 0.296
C×P 0.116
S×C×P 0.694
Effect P
S 0.492
C 0.742
P 0.004
S×C 0.497
S×P 0.660
C×P 0.830
S×C×P 0.726
Effect P
S 0.002
C 0.894
P 0.015
S×C 0.930
S×P 0.672
C×P 0.376
S×C×P 0.202
Effect P
S 0.104
C 0.533
P 0.000
S×C 0.972
S×P 0.114
C×P 0.412
S×C×P 0.385
Effect P
S 0.009
C 0.000
P 0.000
S×C 0.927
S×P 0.007
C×P 0.000
S×C×P 0.051
Effect P
S 0.090
C 0.042
P 0.000
S×C 0.000
S×P 0.008
C×P 0.027
S×C×P 0.000
control
P fertilization
control
P fertilization
control
P fertilization
control
P fertilization
soil of Abies fabri
soil of Picea brachytyla
soil of Abies fabri
soil of Picea brachytyla

Figure 4

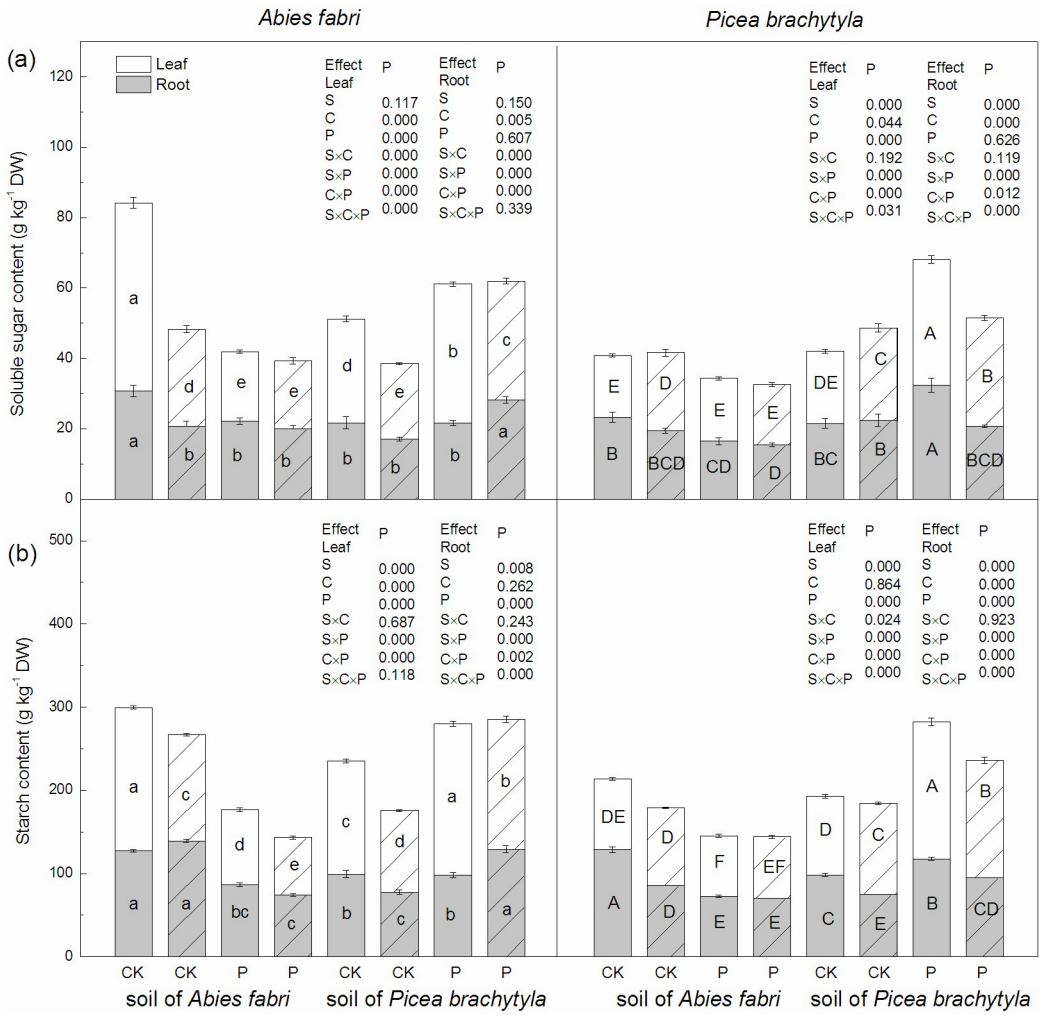

Abies fabri
Picea brachytyla
(a)
(b)
Leaf
Root
Soluble sugar content (g kg-1 DW)
Starch content (g kg-1 DW)
Effect Leaf P
S 0.117
C 0.000
P 0.000
S×C 0.000
S×P 0.000
C×P 0.000
S×C×P 0.000
Effect Root P
S 0.150
C 0.005
P 0.607
S×C 0.000
S×P 0.000
C×P 0.000
S×C×P 0.339
Effect Leaf P
S 0.000
C 0.044
P 0.000
S×C 0.192
S×P 0.000
C×P 0.000
S×C×P 0.031
Effect Root P
S 0.000
C 0.000
P 0.626
S×C 0.119
S×P 0.000
C×P 0.012
S×C×P 0.000
Effect Leaf P
S 0.000
C 0.000
P 0.000
S×C 0.687
S×P 0.000
C×P 0.000
S×C×P 0.118
Effect Root P
S 0.008
C 0.262
P 0.000
S×C 0.243
S×P 0.000
C×P 0.002
S×C×P 0.000
Effect Leaf P
S 0.000
C 0.864
P 0.000
S×C 0.024
S×P 0.000
C×P 0.000
S×C×P 0.000
Effect Root P
S 0.000
C 0.000
P 0.000
S×C 0.923
S×P 0.000
C×P 0.000
S×C×P 0.000
CK CK P P CK CK P P
soil of Abies fabri
soil of Picea brachytyla
soil of Abies fabri
soil of Picea brachytyla

Figure 5

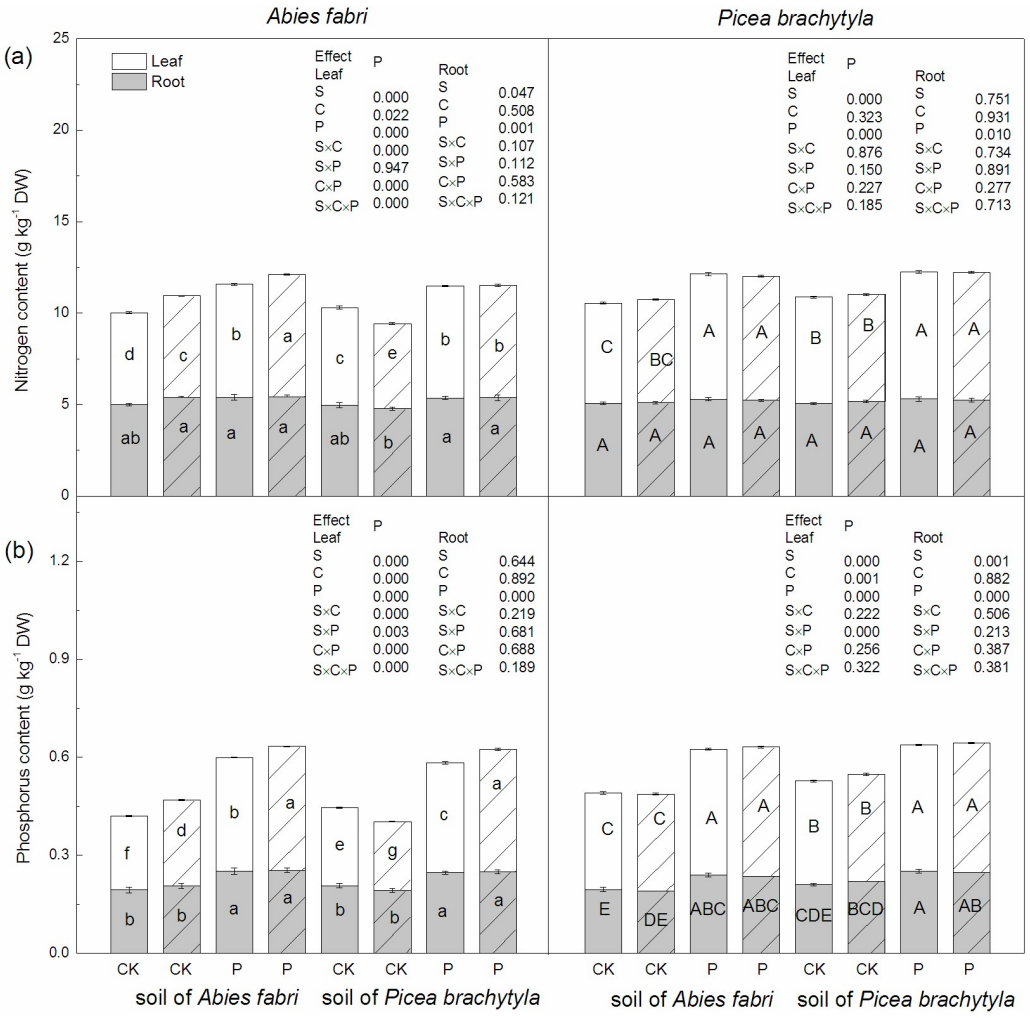
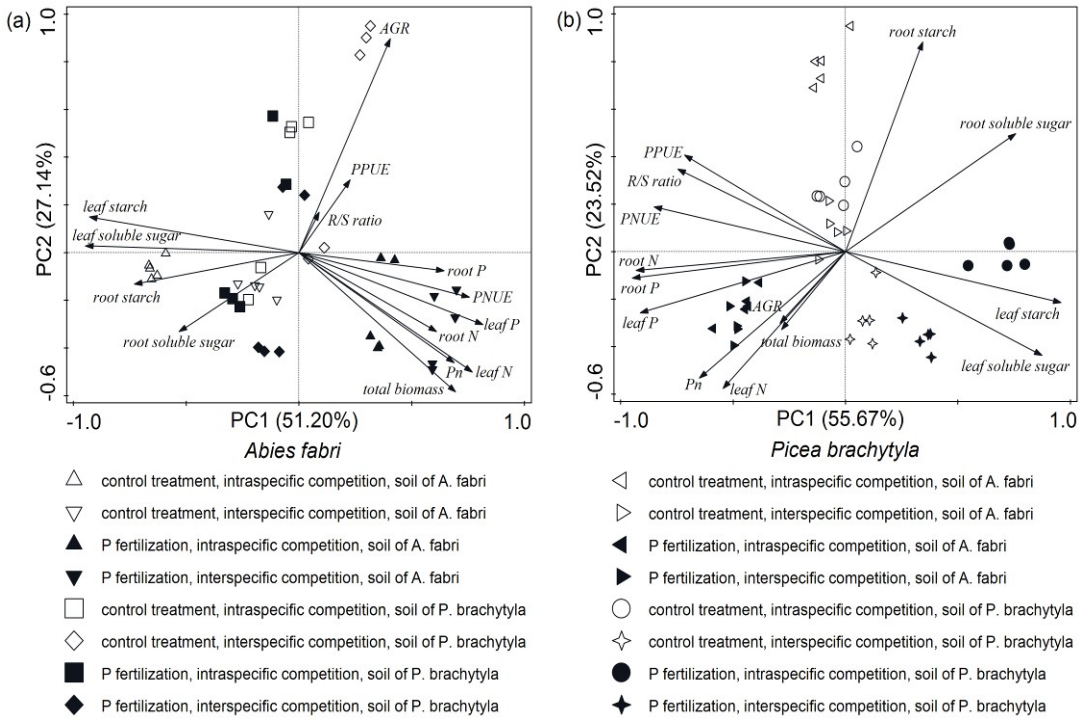

Abies fabri
Picea brachytyla
(a)
(b)
Leaf
Root
Nitrogen content (g kg-1 DW)
Phosphorus content (g kg-1 DW)
Effect P Root
S 0.000 0.047
C 0.022 0.508
P 0.000 0.001
S×C 0.000 0.107
S×P 0.947 0.112
C×P 0.000 0.583
S×C×P 0.000 0.121
Effect P Root
S 0.000 0.751
C 0.323 0.931
P 0.000 0.010
S×C 0.876 0.734
S×P 0.150 0.891
C×P 0.227 0.277
S×C×P 0.185 0.713
Effect P Root
S 0.000 0.644
C 0.000 0.892
P 0.000 0.000
S×C 0.000 0.219
S×P 0.003 0.681
C×P 0.000 0.688
S×C×P 0.000 0.189
Effect P Root
S 0.000 0.001
C 0.001 0.882
P 0.000 0.000
S×C 0.222 0.506
S×P 0.000 0.213
C×P 0.256 0.387
S×C×P 0.322 0.381
CK CK P P CK CK P P
soil of Abies fabri
soil of Picea brachytyla
soil of Abies fabri
soil of Picea brachytyla

Figure 6

1


(a)
1.0
-0.6
PC2 (27.14%)
-1.0
PC1 (51.20%)
1.0
Abies fabri
AGR
PPUE
R/S ratio
leaf starch
leaf soluble sugar
root P
PNUE
leaf P
root starch
root N
root soluble sugar
Pn
leaf N
total biomass
(b)
1.0
-0.6
PC2 (23.52%)
-1.0
PC1 (55.67%)
1.0
Picea brachytyla
root starch
root soluble sugar
PPUE
R/S ratio
PNUE
root N
root P
leaf P
AGR
leaf starch
total biomass
leaf soluble sugar
Pn
leaf N
control treatment, intraspecific competition, soil of A. fabri
control treatment, interspecific competition, soil of A. fabri
P fertilization, intraspecific competition, soil of A. fabri
P fertilization, interspecific competition, soil of A. fabri
control treatment, intraspecific competition, soil of P. brachytyla
control treatment, interspecific competition, soil of P. brachytyla
P fertilization, intraspecific competition, soil of P. brachytyla
P fertilization, interspecific competition, soil of P. brachytyla
control treatment, intraspecific competition, soil of A. fabri
control treatment, interspecific competition, soil of A. fabri
P fertilization, intraspecific competition, soil of A. fabri
P fertilization, interspecific competition, soil of A. fabri
control treatment, intraspecific competition, soil of P. brachytyla
control treatment, interspecific competition, soil of P. brachytyla
P fertilization, intraspecific competition, soil of P. brachytyla
P fertilization, interspecific competition, soil of P. brachytyla

2